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Short Communication

# Temporal variation in invertebrate recruitment on an Eastern Pacific coral reef

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ABSTRACT

The recruitment of marine invertebrate larvae to coral reef ecosystems is critical for the continued productivity of these highly biodiverse habitats. Despite such importance, little is known about temporal variation patterns of invertebrate larval recruitment in coral reefs ecosystems, aside from studies focused only on reef corals themselves. Given this knowledge deficiency, recruitment onto dead coral branches was monitored over a one-year period in the Central Mexican Pacific, and recruit assemblage and density both changed over time. In particular, recruitment was higher in the warmer months, possibly due to reproductive processes and/or increases in metabolic rates associated with high temperatures and seasonal/local events such as upwellings that increase the food resources available for the recruits which just before the warm season, when the recruitment is more more prevalent during the warm season. The most common invertebrate recruits were malacostracans, ostracods, gastropods, maxillopods, and polychaetes, and foraminifers were commonly observed, as well. Future works in this region will seek to understand whether recruit density and diversity change in response to elevated temperatures associated with global climate change.

## 1. Introduction

Coral reef communities are productive ecosystems characterized by high structural complexity (Cortés et al., 2017); they are consequently associated with rich assemblages of both vertebrates and invertebrates (Krieger, 2001). The latter group is more abundant and diverse on coral reefs, with at least 950,000 species of invertebrates having been estimated to reside on, within, or nearby coral reefs (Knowlton and Jackson, 1993; Reaka-Kudla et al., 1996; Glynn and Enochs, 2011). Groups such as crustaceans and mollusks are the most diverse and abundant; they also serve as the prey for a plethora of fish and other invertebrates (Richter et al., 2001). Echinoderms, worms, and sponges are oftentimes present at low densities, though they nevertheless perform important ecological functions in their roles as grazers, detritivores, filter feeders, and nutrient recyclers (Ribes et al., 2005).

Marine invertebrate larval dispersal and recruitment drive changes in abundance, richness and diversity, which thereby influence ecosystem stability and resilience (Caley et al., 1996; Holstein et al., 2014). Recruitment consists of two phases: 1) larval dispersal and 2) attachment onto a suitable substrate that will serve as their permanent residence in the case of sessile organisms (Karlson, 1999). At the physiological level, processes such as reproduction, settlement, and recruitment are affected by seawater quality; temperature (Sanford and Kelly, 2011), salinity, nutrient concentrations, and pH all influence early life history events (Keough and Downes, 1982; Fujisawa and Shigei, 1990; Bourne et al., 2013). Recruitment is also impacted by local and regional oceanographic patterns; such processes determine the rates of larval export and import and therefore the connectivity between populations (Karlson and Hurd, 1999). Biotic factors also influence community structure, and recruitment in particular. For instance, abundance and composition of microbial bio-films, proximity to con-specific adults (Hadfield, 2011), and, in the case of coral reef communities, the presence of photosynthetic symbionts, all affect invertebrate recruitment.

Despite the importance of coral reef invertebrates, the works on functional coral reef invertebrate ecology are primarily restricted to macro-invertebrates, or else invertebrates lumped into a single functional group (e.g., Fabricius et al., 2014; Cortés et al., 2017). Even

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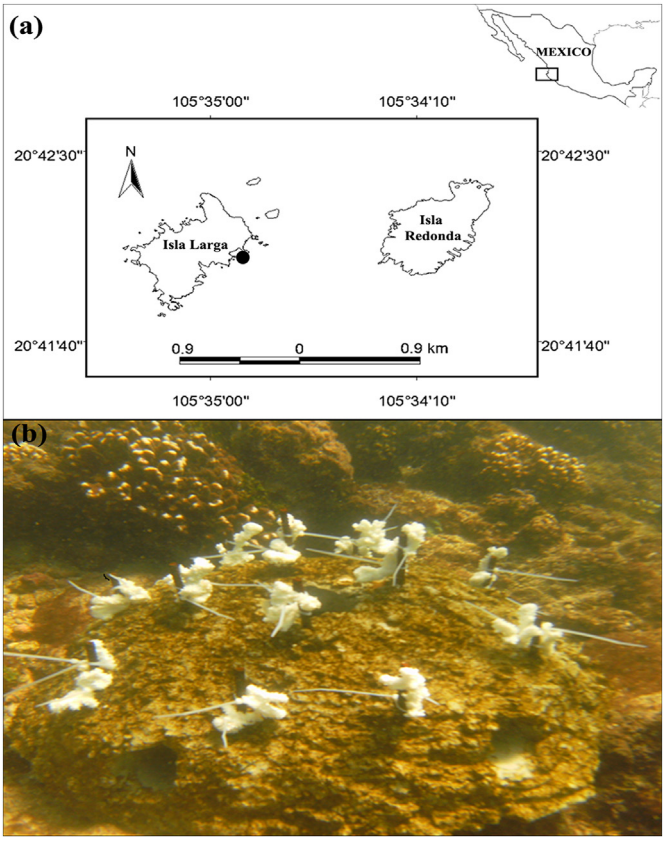


**Fig. 1.** Map of the study site and images of the coral recruitment platform. The study site (a) was located within the Central Mexican Pacific: Islas Marietas National Park. The site of the experiment at Isla Larga is marked with a circle. (b) Semi-spherical concrete structures used as recruitment platforms, with bare coral skeleton fragments attached to steel rods.

presence/absence and density data are typically restricted to a few well studied, conspicuous species, such as hermatypic corals (e.g., Babcock and Mundy, 1996; Miller et al., 2000; Doropoulos et al., 2012; Edmunds et al., 2015; Glynn et al., 2015; Adjeroud et al., 2016). The fact that little recruitment data exist for non-coral marine invertebrates is unfortunate, especially given that such recruitment will not only influence the distribution of the next generation of adults, but it will also affect the abundance and density of organisms at higher trophic levels (Jessen et al., 2014). We sought herein to document multi-month variation in invertebrate recruitment on a coral reef in the Central Mexican Pacific (CMP). We hypothesized that seasonal temperature fluctuations in particular, would influence the recruit assemblage and density.

## 2. Material and methods

The study area, Islas Marietas National Park (IMNP; 20°42′47″-20°41′11”N, 105°33′18″-105°36′00”W; Fig. 1) consists of two small islands of volcanic origin, and the surrounding coral reefs are among the most diverse and well-developed in the CMP region (CONANP, 2007). Sampling was performed at Isla Larga (Fig. 1), which harbors the largest patch reef in the vicinity. This reef is characterized by a high cover of branching corals of the genus *Pocillopora* spp. in the shallows, whereas massive and encrusting species dominate the deeper areas (Hernández-Zulueta et al., 2017). Reefs of IMNP are located in an oceanographic transition area and are influenced annually by the California Current, the Costa Rica Coastal Current, and the waters from the Gulf of California (Palacios-Hernández et al., 2010; Pantoja et al., 2012); furthermore, El Nino Southern Oscillation (ENSO) events can cause both positive and negative thermal anomalies in the area (Wang and Fiedler, 2006). Finally, upwelling and internal waves seasonally influence the area, and they can both inundate reefs with cold, nutrient-rich water (Filonov et al., 1996).

In order to reduce our environmental impact, 119 naturally fragmented, dead pocilloporid coral branches (~5 cm long) were used as recruitment substrata. They were removed from the ocean, submerged in 10% sodium hypochlorite for 24 h to remove all organic material aside from the calcium carbonate skeleton, washed with running fresh water for 8 h, and dried in a convection oven at 60 °C for 24 h.

At the study site, two semi-spherical concrete structures with six steel rods each were placed on a sandy bottom at 5 m depth next to several healthy *Pocillopora* spp. colonies six months prior to monitoring recruitment. The bare coral skeleton fragments were attached to the steel rods with plastic cable tides and left at the site for 60 days. Afterwards, all 119 coral fragments were collected and replaced with another batch of 119 fragments prepared identically. This bimonthly sampling step was initiated in March 2011 and repeated seven times between March 2011 and February 2012; in total 833 coral branches were analyzed. At the time of collection, fragments were packed in plastic bags in situ, transported to the laboratory in an iced cooler, and preserved at −20 °C until further processing.

At a later date, each sample was individually defrosted, and all organisms associated were carefully separated and identified to the lowest level of taxonomic resolution possible according to the following references: Miner (1950), Schultz (1969), Smith (1967), Brusca and Brusca (1990), and Ruppert and Barnes (1995). Recruits were

**Table 1**
One-way nested PERMANOVA of macroinvertebrate richness, density, diversity, dominance, and assemblage. “ST” = sampling time and “C.V.” = coefficient of variation.

| Source of variation | Pseudo-*F* | *p* | C.V. (%) | Source of variation | Pseudo-*F* | *p* | C.V. (%) |
|---|---|---|---|---|---|---|---|
| **Univariate PERMANOVA** | | | | | | | |
| *Macroinvertebrate richness($\bar{S}$)* | | | | *Shannon diversity index (H')* | | | |
| Season | 85.626 | **0.0001** | 40.6 | Season | 0.30394 | 0.584 | 5.8 |
| ST(Season) | 13.575 | **0.0001** | 26.4 | ST(Season) | 13.527 | **0.0001** | 41.8 |
| Residuals | | | 33.0 | Residuals | | | 52.4 |
| *Total invertebrate density (Ind*cm$^{-2}$) ($\overline{N}$)* | | | | *Simpson's dominance (D)* | | | |
| Season | 119.63 | **0.0001** | 42.8 | Season | 5.9475E-4 | 0.9817 | 0.0 |
| ST(Season) | 18.615 | **0.0001** | 27.78 | ST(Season) | 5.3081 | **0.0001** | 31.9 |
| Residuals | | | 29.4 | Residuals | | | 68.1 |
| **PERMANOVA** | | | | | | | |
| *Macroinvertebrate assemblage* | | | | | | | |
| Season | 119.29 | **0.0001** | 45.3 | | | | |
| ST(Season) | 12.159 | **0.0001** | 23.5 | | | | |
| Residuals | | | 31.2 | | | | |

Bold indicates Statistically significant values.

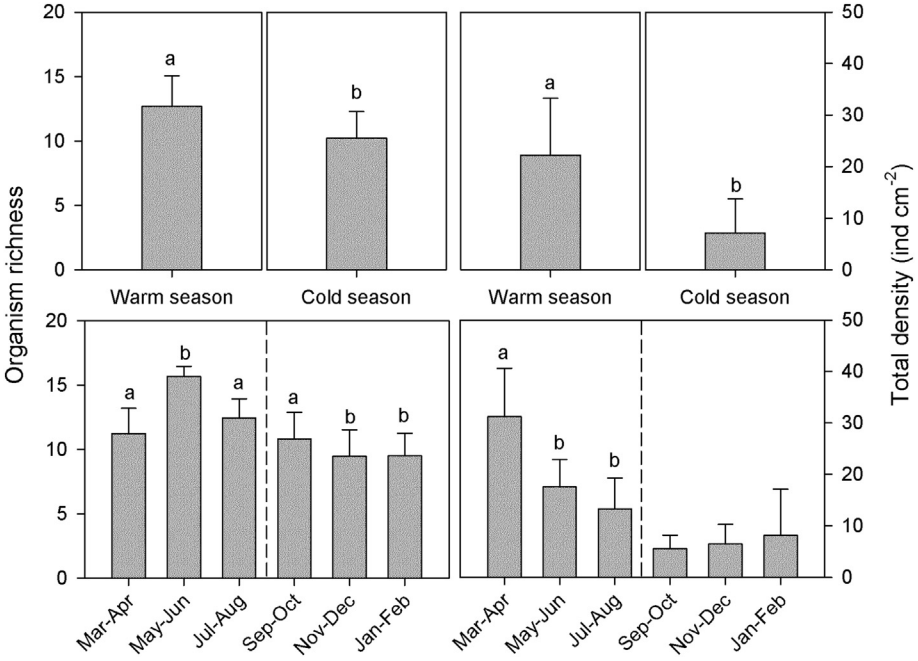


**Fig. 2.** Analysis of invertebrate + foraminifer richness and density. Richness and total abundance were compared across sampling times using a permutational ANOVA. Values represent means ( ± SD), and letters denote significance between individual means (PERMANOVA pseudo-*t post-hoc* test, $p < 0.05$).

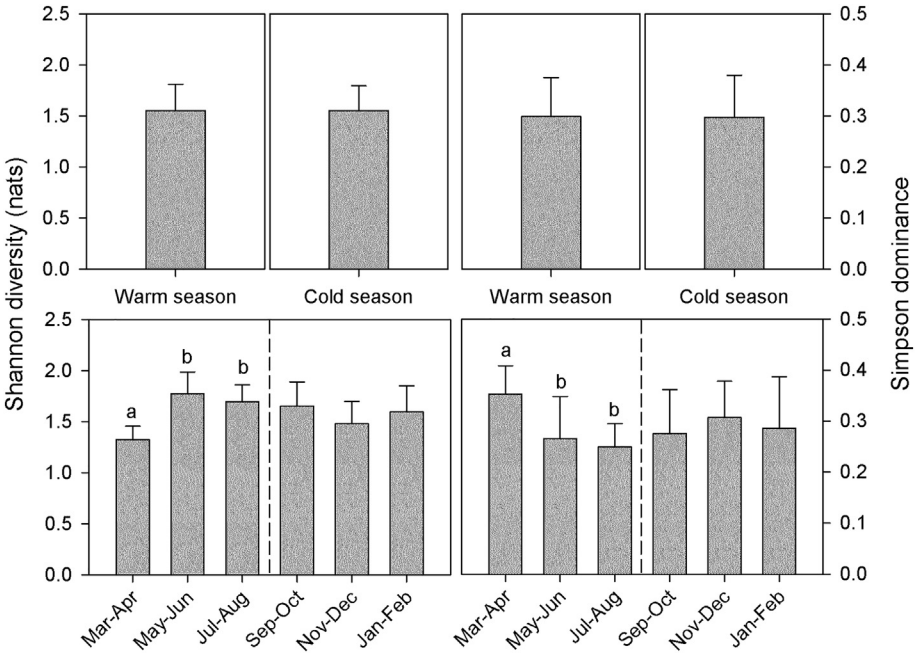


**Fig. 3.** Analysis of invertebrate + foraminifer diversity and dominance. Diversity and dominance were compared across sampling times and seasons with a permutational ANOVA. Values represent means ( ± SD), and letters denote significance between individual means (PERMANOVA pseudo-*t post-hoc* test, $p < 0.05$).

quantified and preserved in a 70% ethanol. Depending on the size of the recruits, either a stereo microscope (Carl Zeiss® Stemi DR-1040) or a compound microscope (LABO® JAZ-ANZ) was used. Algae adhering to the recruitment substrata were not considered.

Abundance data were normalized per available recruitment substrata. Specifically, the area of each coral fragment was estimated using the aluminum foil method described by Marsh (1970), and recruit count data were converted to recruit density by normalizing to surface area (ind·cm$^{-2}$). The in situ seawater temperature at the collection site was registered with a HOBO® Pendant data logger at 15-min intervals. Temperature data are expressed as the mean temperature (°C) ± standard error (SE). As seasonal fluctuations in sea surface temperature were hypothesized to influence the abundance and composition of the micro-invertebrate assemblages, sampling times and data were divided into two seasons: “warm” (March to August) and “cold” (September to February) according to Sotelo-Casas et al. (2016).

Three parameters were calculated to model micro-invertebrate diversity: average richness, the Shannon diversity index (*H'*), and Simpson's dominance (*D*). As the data were neither normally distributed nor homogeneously variable, a one-way, nested permutational univariate analyses of variance (ANOVA) with a fixed-effects model (type I) was used to compare these three diversity indices 1) across times

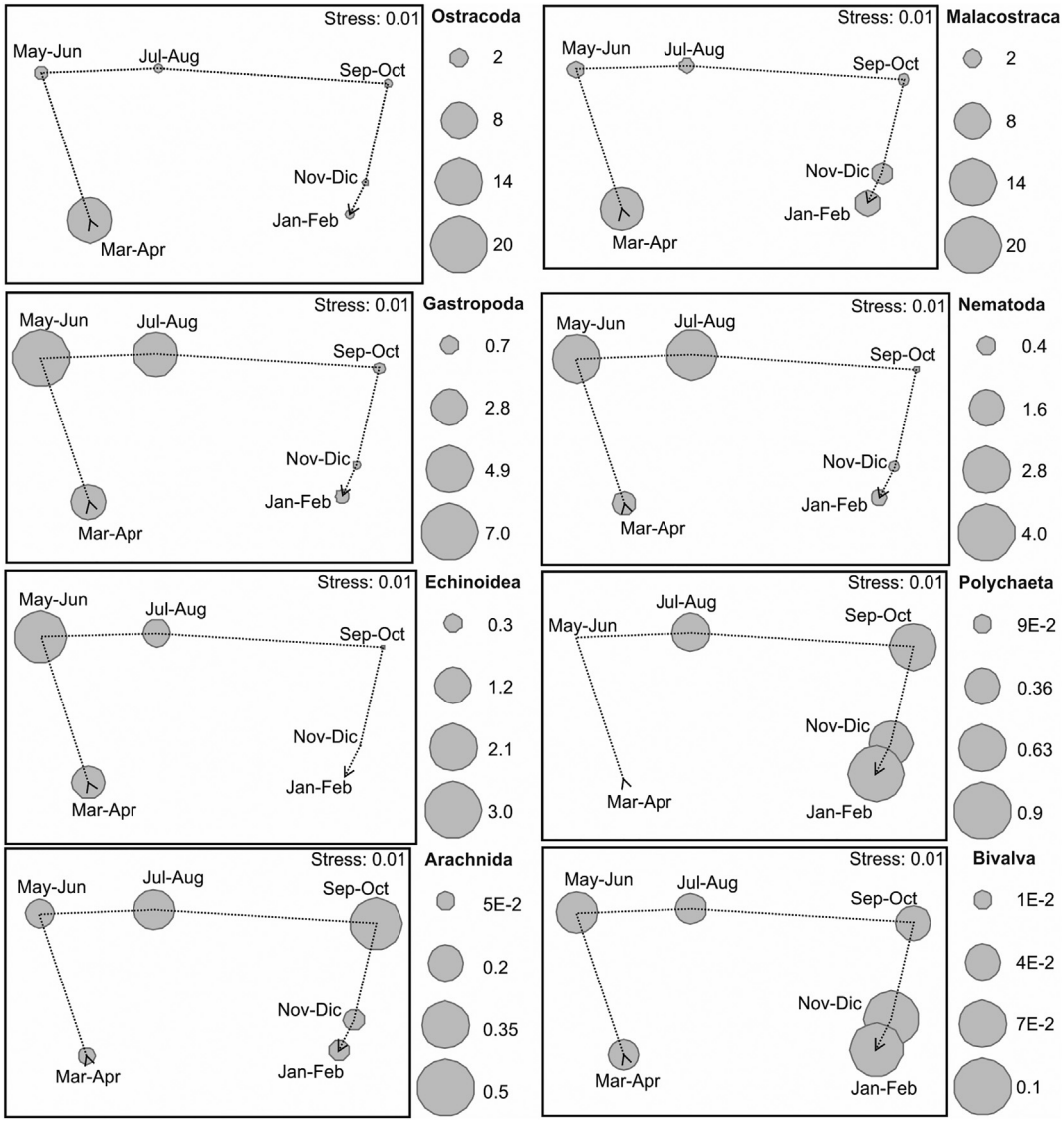


**Fig. 4.** nMDS ordinations-I. Multivariate variation of (A) samples across sampling times and (B) sampling times within the warm (filled icons) and cold (open icons) seasons.

nested within season and 2) between seasons. Afterwards, Euclidean distance matrices were constructed for each diversity index, and the statistical significance was tested using 9999 permutations under a reduced, type III, sum of squares model following the criteria of Anderson et al. (2008). To evaluate invertebrate composition and density variation among sampling times within and between seasons, an additional, nested permutational ANOVA (PERMANOVA; type I model) was performed as described above, albeit instead using a Bray-Curtis similarity matrix constructed with fourth root-transformed data. This transformation was used since the density of the most and least abundant micro-invertebrate taxa differed by several orders of magnitude, and pair-wise comparisons were made with pseudo-*t*-tests.

Similarity and dissimilarity of the invertebrate groups were estimated between sampling times, within seasons (sampling times nested within season), and between seasons using a two-way similarity percentage analysis (SIMPER). A non-metric multidimensional scaling (nMDS) analysis was used to explore multivariate variation of sample assemblages across sampling times and seasons; both SIMPER and nMDS were based on Bray-Curtis similarity matrices using fourth root-transformed data. All univariate and multidimensional analyses were conducted with PRIMER (ver. 6) with the PERMANOVA+ plug-in (Clarke, 1993; Clarke and Warwick, 2001; Anderson et al., 2008), and an alpha level of 0.05 was set a priori for all statistical tests.

## 3. Results

A total of 101,756 invertebrates and foraminifers recruited to 8556.67 $cm^2$ (833 branches) of available coralline substrata over the sampling year. Collected organisms were classified into 20 major taxonomic groups, of which six represented 90% of the total invertebrate abundance and were consistently observed at all survey times; the following four were documented at higher densities in the warm season: malacostracans (11.49 and 0.83 ind·$cm^{-2}$ in the warm and cold seasons, respectively), ostracods (12.45 and 0.19 ind·$cm^{-2}$, respectively), gastropods (6.9 vs. 0.16 ind·$cm^{-2}$, respectively), and polychaetes (2.49 vs. 0.57 ind·$cm^{-2}$, respectively). Of the non-invertebrate taxa observed, foraminifer density presented a similar pattern (4.25 and 0.58 ind·$cm^{-2}$, respectively). Only the maxillopods were documented at a higher density during the cold season (2.29 ind·$cm^{-2}$) vs. 0.62 ind·$cm^{-2}$ during the warm season.

Other taxonomic groups were found at lower densities and were not observed at all sampling periods: Hydrozoa, Anthozoa (solitary anemones only), Anopla, Aphasmidia, Polyplacophora, Bivalva, Monoplacophora, Arachnida, Pycnogonida, Insecta, Echinoidea,

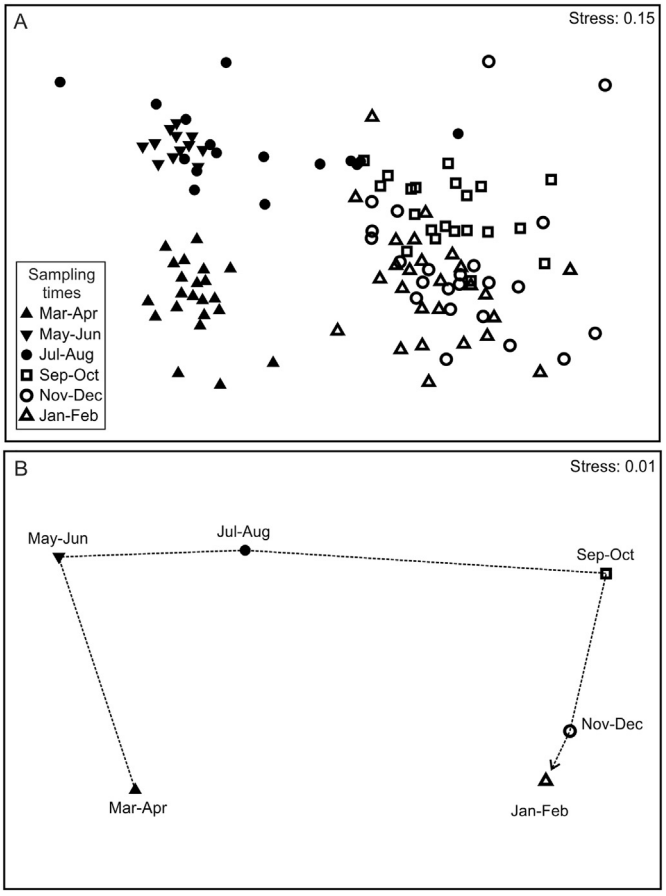


**Fig. 5.** MDS ordination-II. The plots (X-Y) depict the multivariate variation of each of the major groups of invertebrate taxa across sampling times and seasons while panel Z shows the effect of time across all groups analyzed simultaneously.

Ophiuroidea, Holothuroidea, and Gymnolaemata. No coral recruits were observed. The annual average temperature was 26.27 ± 0.02 °C, with the lowest and highest temperatures recorded in February (19.3 ± 0.02 °C) and August (30.2 ± 0.01 °C), respectively. During the warm season, the average temperature was 28.36 ± 0.13 °C, with a minimum recorded during April (20.8 ± 0.02 °C; the transition between cold and warm seasons during which seasonal upwelling occurs for one or two weeks). Finally, the average temperature during the cold season was 25.8 ± 0.01 °C.

Average richness and total abundance differed significantly between seasons (PERMANOVA $p < 0.0001$ and $p < 0.0001$, respectively) and across sampling times within each season ($p < 0.0001$ and $p < 0.0001$, respectively). In contrast, the Shannon diversity index and Simpson's dominance did not differ between seasons, though they did vary across sampling times within seasons (Table 1). Pairwise comparisons revealed that average micro-invertebrate richness and total abundance were higher in the warm season ($\overline{S} = 12.6 \pm 2.3$ and $\overline{N} = 22.2 \pm 11.1$, respectively) than in the cold season ($\overline{S} = 10.2 \pm 2.0$ and $\overline{N} = 12.2 \pm 8.1$, respectively). At sampling time level, all samplings present the major richness and total mean abundance during the warm season. During the May–June period, the highest number of invertebrate groups was quantified ($\overline{S} = 15.3 \pm 0.7$), while total invertebrate abundance ($\overline{N} = 31.2 \pm 9.4$; Fig. 2) and Simpson's dominance (D = 0.34 ± 0.05; Fig. 3) peaked in the March–April period. However, the Shannon diversity index, which varied over time within the warm season, was markedly low (H′ = 1.3 ± 0.1) in March–April. Simpson's dominance also varied during the warm season. During the cold season, the mean species richness differed across sampling periods, with the highest richness documented in September–October ($\overline{S} = 10.8 \pm 2.0$; Fig. 2). When looking at the ANOVA *Pseudo-F* statistics (Table 1), it is clear that invertebrate density and richness varied more across the two seasons, whereas H ‘and D did not (instead varying within seasons).

PERMANOVA of the invertebrate + foraminifer assemblage data revealed significant variation between seasons, as well as across sampling times within seasons (Table 1 and Fig. 4). nMDS was used to depict similarity across sampling times for each of the major taxa (Fig. 4), as well as for the composite assemblage (Fig. 5). In general, there was more variation within the warm season than within the cold season. SIMPER analysis revealed that the invertebrate + foraminifer groups that collectively contributed 65% of the dissimilarity between weather seasons were Echinoidea, Polychaeta, Gastropoda, Ostracoda, Nematoda, Hydrozoa, Malacostraca, and Foraminifera (Table 2). From this group, Gastropoda, Malacostraca, and Ostracoda influenced the mean similarity of the warm season dataset most significantly, whereas Malacostraca, Maxillopoda, and Polychaeta were the most significant drivers of the similarity within the cold season dataset. The taxa that contributed most to the dissimilarity between sampling times where Ostracoda, Malacostraca, Gastropoda, Nematoda, and Echinoidea for the warm season and Polychaeta, Arachnida, and Bivalva for the cold season (Table 3 and Fig. 5).

## 4. Discussion

The highest invertebrate + foraminifer recruit richness and density were documented during the warm season. This is unsurprising given that marine invertebrates typically exhibit a seasonal reproductive cycle, and changes in temperature can trigger physiological processes that promote gamete maturation and release (Hoegh-Guldberg and Pearse, 1995). In general, coral larvae have been found to settle and develop more quickly in the summer season (Keough and Downes, 1982; Bourne et al., 2013); furthermore, temperature is also linked to

**Table 2**
**Results of the similarity percentage analysis (SIMPER) within and between seasons**. Only the invertebrate and foraminifer groups collectively contributing 65% of the average similarity and dissimilarity are presented. “Contrib%” = percent contribution, “Cum%” = cumulative percent contribution, “ASim” = average similarity, and “ADiss” = average dissimilarity.

| Taxa | Contrib% | Cum% | Taxa | Contrib% | Cum.% | Taxa | Contrib% | Cum% |
|---|---|---|---|---|---|---|---|---|
| **Warm season:** ASim = 73.27 | | | **Cold season:** ASim = 74.99 | | | **Warm vs. Cold season:** ADiss = 41.84 | | |
| Gastropoda | 15.49 | 15.49 | Malacostraca | 17.35 | 17.35 | Echinoidea | 11.89 | 11.89 |
| Malacostraca | 15.1 | 30.59 | Maxillopoda | 15.73 | 33.08 | Polychaeta | 10.3 | 22.18 |
| Ostracoda | 12.72 | 43.31 | Polychaeta | 13.77 | 46.85 | Gastropoda | 9.92 | 32.1 |
| Maxillopoda | 10.62 | 53.93 | Foraminifera | 13.66 | 60.51 | Ostracoda | 9.07 | 41.17 |
| Echinoidea | 9.94 | 63.87 | Ostracoda | 9.9 | 70.41 | Nematoda | 7.19 | 48.36 |
| Nematoda | 9.22 | 73.09 | | | | Hydrozoa | 6.88 | 55.25 |
| | | | | | | Malacostraca | 6.16 | 61.41 |
| | | | | | | Foraminifera | 5.26 | 66.67 |

**Table 3**
**Similarity percentage analysis (SIMPER) within and between sampling times.** Only the invertebrate and foraminifer groups collectively contributing 65% of the average similarity and dissimilarity are presented. "Contrib.%" = percent contribution, "Cum%" = cumulative percent contribution, "ADiss" = average dissimilarity, and "ASim" = average similarity.

| Taxa | Contrib.% | Cum% | Taxa | Contrib.% | Cum% | Taxa | Contrib.% | Cum% |
|---|---|---|---|---|---|---|---|---|
| **Sampling dates within the warm season** | | | | | | | | |
| Mar.-Apr: ASim = 80.90 | | | May–June: ASim = 86.59 | | | July-Aug: ASim = 75.06 | | |
| Ostracoda | 20.22 | 20.22 | Gastropoda | 13.83 | 13.83 | Gastropoda | 17.09 | 17.09 |
| Malacostraca | 19.93 | 40.16 | Nematoda | 10.05 | 23.88 | Malacostraca | 13.48 | 30.57 |
| Gastropoda | 12.98 | 53.14 | Echinoidea | 9.91 | 33.79 | Nematoda | 10.58 | 41.15 |
| Maxillopoda | 12.05 | 65.19 | Malacostraca | 9.77 | 43.56 | Maxillopoda | 9.66 | 50.81 |
| | | | Ostracoda | 7.99 | 51.56 | Ostracoda | 9.41 | 60.22 |
| | | | Hydrozoa | 7.22 | 58.78 | Polyplacophora | 7.31 | 67.52 |
| | | | Maxillopoda | 6.72 | 65.49 | | | |
| Mar.-Apr. vs. May–June: ADiss = 30.37 | | | May–June vs. July-Aug: ADiss = 41.52 | | | | | |
| Ostracoda | 12.28 | 12.28 | Hydrozoa | 9.18 | 9.18 | | | |
| Malacostraca | 9.64 | 21.92 | Foraminifera | 8.99 | 18.17 | | | |
| Polyplacophora | 7.9 | 29.82 | Echinoidea | 8.86 | 27.03 | | | |
| Holothuroidea | 7.41 | 37.23 | Nematoda | 8.32 | 35.35 | | | |
| Nematoda | 7.31 | 44.54 | Holothuroidea | 7.78 | 43.13 | | | |
| Ophiuroidea | 7.25 | 51.8 | Polychaeta | 6.33 | 49.46 | | | |
| Hydrozoa | 6.93 | 58.73 | Nemertea | 5.86 | 55.33 | | | |
| Gastropoda | 5.8 | 64.53 | Pycnogonida | 5.29 | 60.61 | | | |
| Nemertea | 4.75 | 69.28 | Anthozoa | 5.24 | 65.85 | | | |
| **Sampling dates within the cold season** | | | | | | | | |
| Sept.-Oct: ASim = 78.69 | | | Nov.-Dec: ASim = 75.05 | | | Jan.-Feb: ASim = 77.43 | | |
| Maxillopoda | 18.27 | 18.27 | Malacostraca | 18.57 | 18.57 | Malacostraca | 18.74 | 18.74 |
| Malacostraca | 14.27 | 32.54 | Maxillopoda | 18.2 | 36.77 | Polychaeta | 14.88 | 33.62 |
| Polychaeta | 12.83 | 45.37 | Foraminifera | 16.35 | 53.12 | Foraminifera | 13.75 | 47.37 |
| Ostracoda | 10.6 | 55.97 | Polychaeta | 12.57 | 65.7 | Maxillopoda | 11.52 | 58.88 |
| Arachnida | 10.38 | 66.35 | | | | Ostracoda | 11.35 | 70.23 |
| Sept.-Oct. vs. Nov.-Dec: ADiss = 26.95 | | | Nov.-Dec. vs. Jan.-Feb: ADiss = 4.94 | | | | | |
| Malacostraca | 10.68 | 10.68 | Malacostraca | 10.92 | 10.92 | | | |
| Arachnida | 10.49 | 21.17 | Ostracoda | 10.16 | 21.08 | | | |
| Foraminifera | 8.58 | 29.75 | Maxillopoda | 8.81 | 29.9 | | | |
| Ostracoda | 8.17 | 37.92 | Gastropoda | 8.46 | 38.35 | | | |
| Gastropoda | 6.93 | 44.84 | Arachnida | 8.01 | 46.36 | | | |
| Maxillopoda | 6.78 | 51.63 | Bivalva | 7.54 | 53.9 | | | |
| Nematoda | 6.57 | 58.19 | Foraminifera | 7.34 | 61.24 | | | |
| Bivalva | 6.22 | 64.42 | Polychaeta | 7.19 | 68.43 | | | |
| Polychaeta | 5.76 | 70.18 | | | | | | |

food availability, which is essential for nourishment of zooplankton, and for the successful recruitment and initial growth of both planktonic and lecitotrophic larvae (Fujisawa and Shigei, 1990; Glynn and Enochs, 2011). However, although nutrient levels, and therefore food availability, are generally attributet to the cold season in the CMP (Palacios-Hernández et al., 2010), internal waves and seasonal upwelling events may occur during the summer in the CMP, producing short-term low temperature events (Filonov et al., 1996); during such periods, nutrient-rich water is made available to larvae. In this study, the low temperature registered during April (21 °C) coincided with the occurrence of upwelling events (data not shown); therefore, it is not possible to determine whether high nutrient levels or the change in season was more important in driving the presumably higher reproductive output that manifested in higher recruit densities. Future works in the CMP should document nutrient levels and temperature to determine which is more important in driving variation in recruit diversity and density.

The invertebrate recruit assemblage differed significantly over time, and, in addition to the aforementioned abiotic effects, such differences may be attributed to either predation or competition. The fact that mollusks, echinoderms, and polychaetes recruited year-round is unsurprising, given that all are important food sources on coral reefs and play key roles in bioerosion, as well. Echinoderms are particularly crucial for controlling the cover of macroalgae and turf algae, both of which compete intensely with corals and can thwart coral recruitment (Alvarado et al., 2016). That being said, the CMP is generally characterized by low densities of adult echinoderms (Sotelo-Casas et al., 2016); too many can actually result in reef-damaging levels of bioerosion (Reaka-Kudla et al., 1996; Glynn et al., 2015; Alvarado et al., 2016), though a certain amount of bioerosion is normal, and even advantageous for many reefs (Scott et al., 1988).

Mollusks are among the most species-rich marine invertebrate phyla on coral reefs (Glynn and Enochs, 2011), and they were the most represented herein. In general, their recruitment and subsequent growth on calcium carbonate rock/substrata occurs only after substrate exposure and pre-conditioning by boring microendolithic organisms and polychaete worms (Hutchings 2011; Alvarado et al., 2016), which also recruited to coral skeletons year-round.

No reef coral recruits, and very few anemone recruits, were found on the coral skeletons. This is puzzling given the abundance of adult corals in the vicinity. Other researchers have documented hard coral settlement on artificial substrata (terracotta tiles, reef balls, etc.) in the region, and recruitment rates $\geq 20$ ind $m^{-2} yr^{-1}$ were documented (Medina-Rosas et al., 2005; López-Pérez et al., 2007; Cabral-Tena et al., 2018). However, on natural substrata, recruitment rates of branching species may be $\leq 1$ ind $m^{-2} yr^{-1}$ (Birkeland, 1977; Richmond, 1985; Guzmán and Cortés, 2001; López-Pérez et al., 2007), though massive and sub-massive species can reach 8 ind $m^{-2} yr^{-1}$ (Reyes-Bonilla and Calderón-Aguilera, 1994; Glynn and Leyte-Morales, 1997; López-Pérez et al., 2007; Glynn et al., 2011; Santiago-Valentín et al. in press). Hard corals tend to settle on crustose coralline algae (CCA), rocks, coral rubble, or dead coral (Santiago-Valentín et al. in press), all of which were found at the study site; perhaps high coral recruitment levels would have been documented on other substrata. However, a previous study concluded that maintenance of Eastern Pacific reefs results from asexual propagation and long-distance dispersal from Central/Western Pacific populations (Glynn et al., 2017); given this, as well as the

absence of coral recruits in our study, the relatively high live coral cover at the field site (Hernández-Zulueta et al., 2017), is clearly not a product of a high degree of self-seeding (within-site recruitment).

Although community composition and abiotic changes could both influence larval recruitment, settlement cues must also be considered. The presence of bacterial biofilms, as well as the microbial assemblage comprising such films, might also change over time; given the importance of such films, as well as a diverse array of CCA, for larval settlement (Hadfield, 2011), and as optimal settlement is caused by complex biochemical communications among CCA, their epiphytic microbial community and invertebrate larvae (Gómez-Lemos et al., 2018); their presence, density, and diversity might have driven, in part, the temporal variation in invertebrate recruitment (in terms of both density and diversity; Kelaher et al., 2001). Future recruitment studies in the CMP (and elsewhere) should not only seek to document the preferred type of bacterial film and/or coralline algae for invertebrate settlement, but should also quantify the degree of algal settlement; although algae can compete with coral and other invertebrates, these invertebrates rely on such algae as a food source as they grow.

The invertebrates associated with the CMP reef surveyed recruited at different rates over the course of the year, and the overall assemblage differed temporally. The survey year was relatively “typical” in terms of temperature fluctuations (Sotelo-Casas et al., 2016). However, large fluctuations or increases in temperature above local averages, such as during ENSO events, can affect reproduction, as well as the physiology and survival of the larvae (Helmuth et al., 2006; Sanford and Kelly, 2011). Future work will seek to document the ability, or lack thereof, of invertebrates to continue to reproduce competent larvae capable of settlement during ENSO events.

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## References

Adjeroud, M., Wallace, C.C., Bosserelle, P., Payri, C., Menou, J.L., Pichon, M., 2016. Reefs at the edge: coral community structure around Rapa, southernmost French Polynesia. Mar. Ecol. 37, 565–575. https://doi.org/10.1111/maec.12308.

Alvarado, J.J., Cortés, J., Guzman, H., Reyes-Bonilla, H., 2016. Bioerosion by the sea urchin *Diadema mexicanum* along Eastern Tropical Pacific coral reefs. Mar. Ecol. 37, 1088–1102. https://doi.org/10.1111/maec.12372.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + Primer: Guide to Software and Statistical Methods. PRIMER-E Ltd, Plymouth, UK.

Babcock, R., Mundy, C., 1996. Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. J. Exp. Mar. Biol. Ecol. 206, 179–201. https://doi.org/10.1016/S0022-0981(96)02622-6.

Birkeland, C., 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. In: Proc 3rd Int Coral Reef Symp (Miami). Vol. 1. pp. 15–21.

Bourne, D.G., Dennis, P.G., Uthicke, S., Soo, R.M., Tyson, G.W., Webster, N., 2013. Coral reef invertebrate microbiomes correlate with the presence of photosymbionts. ISME J. 7, 1452–1458. https://doi.org/10.1038/ismej.2012.172.

Brusca, R.C., Brusca, G.J., 1990. Invertebrates. Sinauer Associates. Sunderland. In: MA.

Cabral-Tena, R.A., DA, Paz-García, Reyes-Bonilla, H., González-Peláez, S.S., Balart, E.F., 2018. Spatio-temporal variability in coral (Anthozoa: Scleractinia) larval recruitment in the southern Gulf of California. Pac. Sci. 72, 435–447. https://doi.org/10.2984/72.4.4.

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. Annu. Rev. Ecol. Syst. 27, 477–500. https://doi.org/10.1146/annurev.ecolsys.27.1.477.

Clarke, K., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x.

Clarke, K., Warwick, R., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Natural Environment Research Council, Plymouth, UK.

CONANP, 2007. Programa de conservación y manejo. In: Parque Nacional Islas Marietas. CONANP/SEMARNAT Press, DF, Mexico.

Cortés, J., Enochs, I.C., Sibaja-Cordero, J., Hernández, L., Alvarado, J.J., Breedy, O., Antonio Cruz-Barraza, José, Esquivel-Garrote, O., Fernández-García, F., Hermosillo, A., Kaiser, K.L., Medina-Rosas, P., Morales-Ramírez, A., Pacheco, C., Pérez-Matus, A., Reyes-Bonilla, H., Riosmena-Rodríguez, R., Sánchez-Noguera, C., Wieters, E.A., Zapata, F.A., 2017. Marine biodiversity of Eastern Tropical Pacific coral reefs. In: Glynn, P.W., Manzello, D.P., Enochs, I.C. (Eds.), Coral Reefs of the Eastern Tropical Pacific. Springer Netherlands, pp. 203–250.

Doropoulos, C., Ward, S., Díaz-Pulido, G., Hoegh-Guldberg, V., Mumby, P.J., 2012. Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. Ecol. Lett. 15, 338–346. https://doi.org/10.1111/j.1461-0248.2012.01743.x.

Edmunds, P.J., Steneck, R., Albright, R., Carpenter, R.C., Chui, A.P.Y., Fan, T.Y., Harii, S., Kitano, H., Kurihara, H., Legendre, L., Mitarai, S., Muko, S., Nozawa, Y., Padilla-Gamino, J., Price, N.N., Sakai, K., Suzuki, G., van Oppen, M.J.H., Yarid, A., Gates, R.D., 2015. Geographic variation in long-term trajectories of change in coral recruitment: a global-to-local perspective. Mar. Freshw. Res. 66, 609–622. https://doi.org/10.1071/MF14139.

Fabricius, K.E., De'ath, G., Noonan, S., Uthicke, S., 2014. Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. Proc. R. Soc. B 281, 20132479. https://doi.org/10.1098/rspb.2013.2479.

Filonov, A., Monzon, C., Tereshschenko, I., 1996. On the conditions of internal tide wave generation along the west coast of Mexico. Ciencias Marinas 22, 255–272.

Fujisawa, H., Shigei, M., 1990. Correlation of embryonic temperature sensitivity of sea urchins with spawning season. J. Exp. Mar. Biol. Ecol. 136, 123–139. https://doi.org/10.1016/0022-0981(90)90191-E.

Glynn, P.W., Enochs, I.C., 2011. Invertebrates and their roles in coral reef ecosystems. In: Dubinsky, Z., Stambler, N. (Eds.), Coral Reefs: An Ecosystem in Transition. Springer Press, Dordrecht, pp. 273–325. https://doi.org/10.1007/978-94-007-0114-4_18.

Glynn, P.W., Leyte-Morales, G.E., 1997. Coral reefs of Huatulco, West México: reef development in upwelling Gulf of Tehuantepec. Rev. Biol. Trop. 45, 1033–1047.

Glynn, P.W., Colley, S.B., Guzmán, H.M., Enochs, I.C., Cortés, J., Maté, J.L., Feingold, J., 2011. Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá and the Galápagos Islands (Ecuador). VI. Agariciidae, *Pavona clavus*. Mar. Biol. 158, 1601–1617. https://doi.org/10.1007/s00227-011-1673-z.

Glynn, P.W., Riegl, B.M., Purkis, S., Kerr, J., Smith, T., 2015. Coral reef recovery in the Galápagos Islands: the northern-most islands (Darwin and Wenman). Coral Reefs 34, 421–436 (doi:10.1007/s00338-015-1280-4).

Glynn, P.W., Colley, S.B., Carpizo-Ituarte, E., Richmond, R.H., 2017. Coral reproduction in the eastern Pacific. In: Glynn, P.W., Manzello, D.P., Enochs, I.C. (Eds.), Coral Reefs of the Eastern Tropical Pacific: Persistence and Loss in a Dynamic Environment, Coral Reefs of the World 8. Springer, Dordrecht.

Gómez-Lemos, L.A., Doropoulos, C., Bayraktarov, E., Díaz-Pulido, G., 2018. Coralline algal metabolites induce settlement and mediate the inductive effect of epiphytic microbes on coral larvae. Sci. Rep. 8, 17557. https://doi.org/10.1038/s41598-018-35206-9.

Guzmán, H.M., Cortés, J., 2001. Changes in reef community structure after fifteen years of natural disturbances in the eastern Pacific (Costa Rica). Bull. Mar. Sci. 69, 133–149.

Hadfield, M.G., 2011. Biofilms and marine invertebrate larvae: what bacteria produce that larvae use to choose settlement sites. Annu. Rev. Mar. Sci. 3, 453–470. https://doi.org/10.1146/annurev-,arome-120709-142753.

Helmuth, B., Broitman, B.R., Blanchette, C.A., Gilman, S.E., Hapin, P., O'Donnell, M.J., Hofmann, G.E., Menge, E., Strickland, D., 2006. Mosaic patterns of thermal stress in the Lathlean & Minchinton: thermal stress on rocky shores rocky intertidal zone: implications for climate change. Ecol. Monogr. 76, 461–479. https://doi.org/10.1890/0012-9615(2006)076[0461:MPOTSI]2.0.CO;2.

Hernández-Zulueta, J., Rodríguez-Zaragoza, F., Araya, R., Vargas-Ponce, O., Rodríguez-Troncoso, A.P., Cupul-Magaña, A.L., Díaz-Pérez, L., Ríos-Jara, E., Ortíz, M., 2017. Multi-scale analysis of hermatypic coral assemblages at Mexican Central Pacific. Sci. Mar. 81, 91–102. https://doi.org/10.3989/scimar.04371.12A.

Hoegh-Guldberg, O., Pearse, J., 1995. Temperature, food availability, and the development of marine invertebrate larvae. Am. Zool. 35, 415–425. https://doi.org/10.1093/icb/35.4.415.

Holstein, D.M., Paris, C.B., Mumby, P.J, 2014. Consistency and inconsistency in multispecies population network dynamics of coral reef. Mar. Ecol. Prog. Ser. 499, 1–18. https://doi.org/10.3354/meps10647.

Jessen, C., Voolstra, C.R., Wild, C., 2014. *in situ* effects of simulated overfishing and eutrophication on settlement of benthic coral reef invertebrates in the Central Red Sea. PeerJ 2, e339 (doi:10.7717/peerj.339).

Karlson, R.H., 1999. Dynamics of Coral Communities. Kluwer Academic Publishers, London, UK.

Karlson, R., Hurd, L., 1999. Disturbance, coral reef communities and changing ecological paradigms. Coral Reefs 12, 117–125. https://doi.org/10.1007/BF00334469.

Kelaher, B.P., Chapman, M.G., Underwood, A.J., 2001. Spatial patterns of diverse macrofaunal assemblages in coralline turf and their associations with environmental variables. J. Mar. Biol. Assoc. UK 81, 917–930. https://doi.org/10.1017/S0025315401004842.

Keough, M.J., Downes, B.J., 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia 54, 348–352. https://doi.org/10.1007/BF00380003.

Knowlton, N., Jackson, J.B.C., 1993. Inbreeding and outbreeding in marine invertebrates. In: Thornhill, N.W. (Ed.), The Natural History of Inbreeding and Outbreeding. Chicago Press, NW, pp. 200–249.

Krieger, K.G., 2001. Coral (Primnoa) impacted by fishing gear in the Gulf of Alaska. In: Willison, J.H.J., Hall, S.E., Gass, E.L.R., Kenchington, P., Doherty, P. (Eds.), Proc 1st Int Symp Deep Sea Corals. Ecology Action Centre and Nova Scotia Museum, Halifax, NE, pp. 106–116.

López-Pérez, R.A., Mora-Pérez, M.G., GE, Leyte-Morales, 2007. Coral (Anthozoa: Scleractinia) recruitment at Bahías de Huatulco, Western Mexico: implications for coral community structure and dynamics. Pac. Sci. 61, 355–369. https://doi.org/10.2984/1534-6188(2007)61[355:CASRAB]2.0.CO;2.

Marsh, J.A., 1970. Primary productivity of reef-building calcareous red algae. Ecology 51, 255–263. https://doi.org/10.2307/1933661.

Medina-Rosas, P., Carriquiry, J., Cupul-Magaña, A., 2005. Recruitment of *Porites* (Scleractinia) on artificial substrata in reefs affected by the 1997–98 El Niño in Banderas Bay. Mexican Pacific. Ciencias Marinas 31, 103–109.

Miller, E.W., Weill, E., Szmant, A., 2000. Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayane National Park, USA. Coral reefs 19, 115–123.

Miner, R.W., 1950. Field Book of Seashore Life. GP Putnam's Sons, NY.

Palacios-Hernández, E., Carrillo, L.E., Filonov, A., Brito-Castillo, L., Cabrera-Ramos, C.E., 2010. Seasonality and anomalies of sea surface temperature off the coast of Nayarit. Mexico. Ocean Dyn. 60, 81–91. https://doi.org/10.1007/s10236-009-0244-z.

Pantoja, D.A., Marinone, S., Parés-Sierra, A., Gómez-Valdivia, F., 2012. Numerical modeling of seasonal and mesoscale hydrography and circulation in the Mexican Central Pacific. Ciencias Marinas 38, 363–379 (doi:10.773/c.v38i2.2007).

Reaka-Kudla, M.L., Feingold, J.S., Glynn, P.W., 1996. Experimental studies of rapid bioerosion of coral reefs in the Galápagos Islands. Coral Reefs 15, 101–107. https://doi.org/10.1007/BF01771898.

Reyes-Bonilla, H., Calderón-Aguilera, L.E., 1994. Parámetros poblacionales de *Porites panamensis* (Anthozoa: Scleractinia), en el arrecife de Cabo Pulmo. México. Rev Biol Trop 42, 121–128.

Ribes, M., Coma, R., Atkinson, M.J., Kinzie, R.A., 2005. Sponges and ascidians control removal of particulate organic nitrogen from coral reef water. Limnol. Oceanogr. 50, 1480–1489. https://doi.org/10.4319/lo.2005.50.5.1480.

Richmond, R.H., 1985. Variations in the population biology of *Pocillopora damicornis* across the Pacific. In: Proc 5th Int Coral Reef Congr (Tahiti). Vol. 6. pp. 101–106.

Richter, C., Wunsch, M., Rasheed, M., Kotter, I., Badran, M.I., 2001. Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. Nature 413, 7260730. https://doi.org/10.1038/35099547.

Ruppert, E., Barnes, R., 1995. Zoología de los invertebrados. McGraw-Hill Interamericana, Mexico, D.F.

Sanford, E., Kelly, M.W., 2011. Local adaptation in marine invertebrates. Annu. Rev. Mar. Sci. 3, 509–535. https://doi.org/10.1146/annurev-marine-120709-142756.

Santiago-Valentín, J.D., Rodríguez-Troncoso, A.P., Bautista-Guerrero, E., López-Pérez, R.A., Cupul-Magaña, A.L., 2018. Successful sexual reproduction of the scleractinian coral *Porites panamensis*: evidence of planktonic larvae, and recruitment. Invertebr. Biol (in press).

Schultz, G.A., 1969. How to Know the Marine Isopod Crustaceans. WMC Brown, Dubuque, Iowa.

Scott, P.J.B., Risk, M.J., Carriquiry, J.D., 1988. El Niño, bioerosion and the survival of East Pacific reefs. In: Proc 6th Int Coral Reef Symp (Townsville). Vol. 2. pp. 517–520.

Smith, D.L., 1967. A Guide to Marine Coastal Plankton and Marine Invertebrate Larvae. Kendall/Hunt, Dubuque, Iowa.

Sotelo-Casas, R.C., Cupul-Magaña, A.L., Rodríguez-Zaragoza, F.A., Solís-Marín, F.A., Rodríguez-Troncoso, A.P., 2016. Structural and environmental effects on an assemblage of echinoderms associated with a coral community. Mar. Biodivers. https://doi.org/10.1007/s12526-016-0622-y.

Wang, C., Fiedler, P.C., 2006. ENSO variability and the eastern tropical Pacific: a review. Prog. Oceanogr. 69, 239–266. https://doi.org/10.1016/j.pocean.2006.03.004.